

# Controls of Bedrock Geochemistry on Soil and Plant Nutrients in Southeastern Utah

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## ABSTRACT

The cold deserts of the Colorado Plateau contain numerous geologically and geochemically distinct sedimentary bedrock types. In the area near Canyonlands National Park in Southeastern Utah, geochemical variation in geologic substrates is related to the depositional environment with higher concentrations of Fe, Al, P, K, and Mg in sediments deposited in alluvial or marine environments and lower concentrations in bedrock derived from eolian sand dunes. Availability of soil nutrients to vegetation is also controlled by the formation of secondary minerals, particularly for P and Ca availability, which, in some geologic settings, appears closely related to variation of CaCO<sub>3</sub> and Ca-phosphates in soils. However, the results of this study also indicate that P content is related to bedrock and soil Fe and Al content suggesting that the deposition history of the bedrock and the presence of P-bearing Fe and Al minerals, is important to contemporary P cycling in this region. The relation between bedrock type and exchangeable Mg and K is less clear-cut, despite large

variation in bedrock concentrations of these elements. We examined soil nutrient concentrations and foliar nutrient concentration of grasses, shrubs, conifers, and forbs in four geochemically distinct field sites. All four of the functional plant groups had similar proportional responses to variation in soil nutrient availability despite large absolute differences in foliar nutrient concentrations and stoichiometry across species. Foliar P concentration (normalized to N) in particular showed relatively small variation across different geochemical settings despite large variation in soil P availability in these study sites. The limited foliar variation in bedrock-derived nutrients suggests that the dominant plant species in this dryland setting have a remarkably strong capacity to maintain foliar chemistry ratios despite large underlying differences in soil nutrient availability.

**Key words:** desert; nutrient; soil; foliar; stoichiometry; bedrock.

## INTRODUCTION

The arid ecosystems of the Colorado Plateau have developed on a wide variety of sedimentary bedrock types that range from relatively nutrient-rich

to exceptionally nutrient-poor substrates. This diversity of parent material chemistry, including variation in nutrients such as P, Ca, K, and Mg, may influence ecosystem dynamics through soil-nutrient availability (Schlesinger and Pilmanis 1998). Nutrient availability can be particularly low in arid environments where low precipitation and relatively rapid decomposition lead to slow rates of

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mineral weathering and small stocks of soil organic matter (Noy-Meir 1973; Schlesinger and others 1996; Fernandez and others 2005). Several studies show that available N and P are low in desert regions (James and Jurinak 1978; Gutierrez and Whitford 1987; Fisher and others 1988), even though some deserts have relatively high rates of N fixation through biological soil crusts (Belnap 2001). Arid lands may also have high rates of eolian dust input that enrich surface soils in some essential elements (for example, Reynolds and others 2006) but are also prone to nutrient loss due to wind erosion following land-use change that results in substantial losses of essential, rock-derived nutrients for plants (Neff and others 2005). The substantial spatial variation in bedrock chemistry and the potential for soils to lose rock-derived nutrients through deposition and erosion raise the question of how desert plants respond to changes in nutrients across landscapes or through time.

Plant availability of the rock-derived elements including P, Ca, Mg, and K is controlled by the weathering of minerals. For P in particular, there may be large variations in availability across arid landscapes. Work in arid soils in New Mexico showed large variation in P content and availability across landscapes (Lajtha and Schlesinger 1988a) and illustrated that shrub foliar P content and P uptake rates are controlled by the reactions of phosphate and calcium (Lajtha and Schlesinger 1988b). Studies of desert shrubs also indicate species-level variation in foliar N:P ratios and species-specific growth responses to N or P fertilization (Drenovsky and Richards 2004) or to a combination of N, P, and Mg (James and others 2005). Given the relatively large inputs of N to soils from biological soil crusts (Belnap 2001), previous research suggests that the differences in P and  $\text{CaCO}_3$  across substrates could be particularly important biogeochemical controls of dryland plant nutrient dynamics and vegetation composition.

Arid-land vegetation communities have relatively low diversity, but include broad representation of different plant life forms including grasses, shrubs, forbs, and trees. Historically, the presence or absence of specific species in arid and semi-arid environments has been used to map the occurrence of specific mineral resources as well as to identify and map particular soil types and settings (Soil Survey Division Staff 1993). In semi-arid regions there is evidence that vegetation composition varies with the type of underlying bedrock and evidence for a link between endemism and geologic setting (Wright and Mooney 1965; Nelson and Harper 1991; Ernst and others 2003; James and others

2005). However, there is still limited understanding of the biogeochemical or hydrologic reasons for associations between particular plant species and geologic settings. One notable difference between arid environments and more mesic environments is the intense wind scouring and UV input to the soil surface that results in rapid litter breakdown and dispersal (Whitford 2002). In contrast to more mesic systems, the lack of a litter layer under dryland plants may reduce the importance of plant litter—soil nutrient feedbacks that can be important in mesic to wet environments (Meier and others 2005) and thus increase the comparative importance of nutrient release from parent materials.

Plant nutrient use is an important control over a range of ecosystem processes and there has been much work examining how plants respond to gradients in nutrient availability. There are a number of different techniques that can be used to assess patterns in nutrient use in response to variation in soil nutrient content including fertilization studies, meta-analysis of data, and studies on natural fertility gradients. Of these approaches, fertilization provides the most conclusive evidence of what element limits productivity but also typically requires the addition of nutrients in amounts that greatly exceed natural levels. In comparison, studies of natural fertility gradients offer less direct evidence of limitation but are a useful way to evaluate how species respond to smaller (and more natural) levels of soil nutrient availability. Based on both types of studies, there is strong evidence that plant response to soil nutrient availability is controlled, at least in part, by genetic factors. In particular, species or life forms adapted to low-nutrient environments may be constrained in their ability to absorb and use nutrients, even when those nutrients are available in abundance (Chapin 1980; Lambers and Poorter 1992; Aerts and Chapin 2000). The physiological basis for limited plasticity in foliar nutrient use may occur because plants from low-nutrient settings have greater investment in cell wall materials with relatively fixed element ratios and lower potential relative growth rates (RGR) compared to plants adapted to higher nutrient settings (Van Arendonk and Poorter 1994). This type of plant nutrient use should be manifest as relatively constant foliar nutrient ratios, despite differences in soil nutrient availability. There is evidence for this type of plant response to soil N and P variations (Bowman and others 2003) and for some essential elements in European forests (Meerts 1997; Meier and others 2005). In general however, there is very limited information as to how plants respond to variation in bedrock-derived nutrients and whether variation in

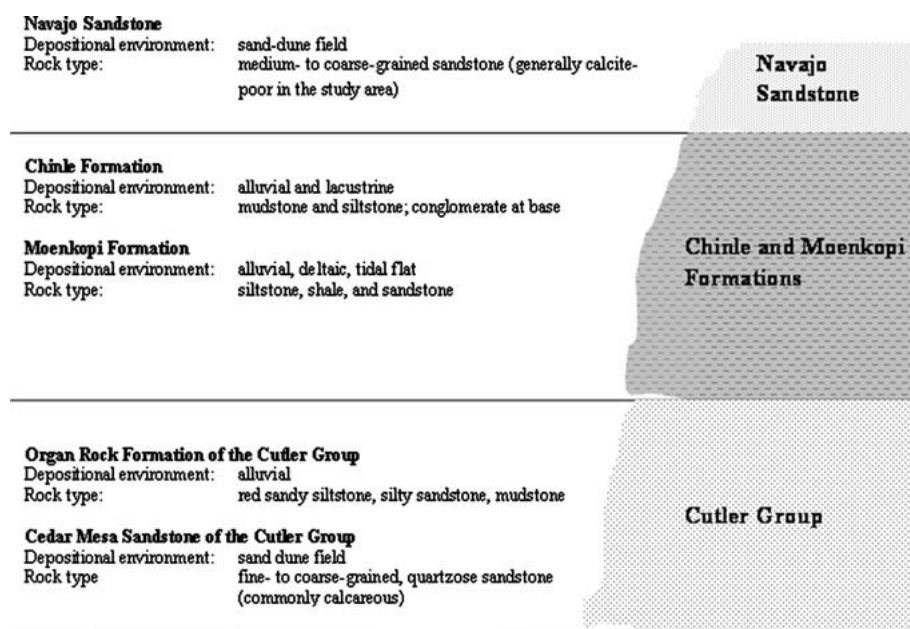


Figure 1. Illustration of the rock units, their depositional environments, and some lithologic properties examined in this paper. The figure illustrates the relative stratigraphic position of each geologic unit relative to the others but not necessarily elevation because of other geologic processes at work in the region.

substrate chemistry translates into variation in plant foliar nutrient concentrations.

Several factors complicate evaluation of plant-nutrient concentration and co-variation with soil-nutrient content. First, different plant species and functional types have differing leaf characteristics that result in large differences in absolute foliar nutrient content (but which provide limited information about plant response to soil-nutrient variation). Second, there are few quantitative metrics available to evaluate variation in tissue-nutrient content (for example, what constitutes significant variation in tissue-nutrient content across species or fertility gradients). The first factor can be addressed partially by examining stoichiometry rather than absolute variation in tissue-nutrient content (Sternner and Elser 2002) and normalizing element ratios to N or P rather than to C, because of the large role and high variability of carbon as a component of structural material across different plant species (Knecht and Göransson 2004). The second issue above is difficult to address comprehensively in a single study, but requires quantitative comparisons of variation in tissue and available soil nutrients across small (local) and large (geographic) fertility gradients.

Here, we examine how the pools of essential plant elements vary across the geologically complex landscapes of Southeastern Utah, and we evaluate what geochemical factors control this variation. Second, we measure plant foliar nutrients to test for parallels with underlying differences in bedrock geochemistry. Finally, we evaluate whether plant species and functional

types respond similarly to variation in bedrock geochemistry and whether this response differs by element (for example, P vs. Ca vs. Mg.) These questions are addressed through a series of measurements of bedrock, soil, and plant chemistry in settings of differing bedrock geochemistry. We focus on the essential, but typically non-limiting, elements such as Ca, Mg, K, and P because they are closely controlled by soil mineral nutrient content and vary significantly with geology across the deserts of the Colorado Plateau.

## METHODS

### Site Characteristics

The four substrates for this study were located at approximately 1,500 m elevation for the Cedar Mesa Sandstone, Organ Rock Formation, and Moenkopi/Chinle Formations, and approximately 2,000 m for the Navajo Sandstone site. These sites are located near Moab, Utah in cold xeric ecosystems in the Needles and Island in the Sky districts of Canyonlands National Park (CNP) (Figure 1). The bedding of the sedimentary rocks in the study area is nearly horizontal; therefore, it is possible to find soils derived mostly from a single geologic/geochemical setting. Soil and vegetation characteristics for the study sites cover the full range of conditions found on the Colorado Plateau (Figure 1; Table 1). Average annual precipitation and temperature in the region is approximately 216 mm and 12°C, respectively (<http://www.wrcc.dri.edu/summary/climsmut.html>).

Table 1. Soil Properties at each Sampling Site

	Cedar Mesa (0–5 cm)	Cedar Mesa (5–10 cm)	Organ Rock (0–5 cm)	Organ Rock (5–10 cm)	Chinle/Moenkopi (0–5 cm)	Chinle/Moenkopi (5–10 cm)	Navajo (0–5 cm)	Navajo (5–10 cm)
Soil % organic C content	0.21 (0.04)	0.22 (0.01)	0.15 (0.02)	0.22 (0.02)	0.21 (0.04)	0.17 (0.01)	0.36 (0.04)	0.23 (0.02)
Soil total N content (%)	0.019 (0.001)	0.019 (0.001)	0.011 (0.01)	0.019 (0.02)	0.023 (0.003)	0.020 (0.002)	0.028 (0.003)	0.021 (0.002)
C:N ratio	11.0 (1.0)	11.5 (0.2)	10.7 (0.6)	11.5 (2.2)	8.9 (0.7)	8.9 (0.8)	12.8 (0.4)	10.8 (0.1)
Soil carbonate content (%)	6.98 (2.02)	6.96 (1.83)	7.24 (1.08)	7.76 (1.00)	16.50 (7.17)	15.43 (6.39)	0.37 (0.11)	0.59 (0.22)
Cation exchange capacity (cmol/Kg)	5.69 (0.42)	ND	5.56 (0.59)	ND	8.03 (0.81)	ND	5.05 (0.56)	ND
Sand:silt:clay content	72:20:8	72:20:8	72:20:8	75:17:8	63:24:13	62:25:13	81:14:5	84:11:5

*Average organic C, N, carbonate, and texture for all sites within a particular bedrock setting. Values in parentheses are standard errors (n = 3).*

## Field Sampling

We established three 40 × 40 m plots within each geologic setting (substrate) making three true replicate plots for each substrate. These replicate plots were located in approximately the same stratigraphic section of each formation to ensure general geochemical similarity between the sites. Each of the sites were separated from one another by 0.5–5 km. We sampled exposed rock outcrops for bedrock collection at each site. Because the outcrops are not uniform across the landscape, we could not obtain equal numbers of rock samples for each geologic setting. We analyzed four bedrock samples in the Cedar Mesa Sandstone, five outcrops in the Organ Rock Formation, two outcrops in the Navajo Sandstone, and three outcrops in the Moenkopi/Chinle Formations. The soils are attributed to weathering of a distinct bedrock unit within each geologic setting with the exception of the Moenkopi/Chinle site where soils are derived from mixed sources in both underlying and nearby bedrock sources located on steep hillslopes above the plot locations. These units are referred to as the Moenkopi/Chinle settings because of the varied contributions of these two geologic units to soils.

All four sites were established in areas that were either actively or historically grazed and were sampled when no cattle were present (the actively grazed sites are stocked only for several weeks out of the year). At each site we composited three soil and foliage subsamples to obtain one sample of soil and one sample of foliage for analysis per site. There were a total of three sites sampled for each geologic setting. A bulk density corer was used to collect soils at 0–5 cm and 5–10 cm. These layers correspond roughly to the A horizon and the Bw horizon. Unlike many mesic ecosystems, there are not standing litter layers on these sites so soils were sampled from near the top of the soil column. There were no obvious differences in surface soil horizons across the sites although the depth and size of calcic horizon at more than 20 cm does vary between sites. Soils on the Cedar Mesa Sandstone were generally classified as Begay fine sand loams (Ustic Haplocambids). Soils on the Organ Rock substrates are the Nakai fine sand (Typic Haplocalcids) and Thorofare fine sandy loam (Typic Torrifluvents) classifications. Soils derived from Moenkopi/Chinle Formations were classified as Nakai fine sands, and soils on the Navajo Sandstone site were in the Begay fine sandy loam series (U.S. Department of Agriculture Soil Conservation Service 1991).

We sampled leaf tissue from ten plant species that represent the dominant species across these sites. Four of the plant species occurred in each of the four geologic settings; blackbrush (*Coleogyne ramosissima*), snakeweed (*Gutierrezia sarothrae*), a native bunchgrass (*Stipa hymenoides*), and four wing saltbush (*Atriplex canescens*). The leaf tissue for all plants was sampled prior to senescence within a 2-day period in early October, following a post-monsoonal growth period. Although we cannot comment on annual nutrient use in this study, the results should reflect a period of relatively high decomposition and nutrient availability in these systems (Fernandez and others 2005). To ensure that plant water use differences were not responsible for variation across the geologic settings, we carried out analysis of plant  $\delta^{13}\text{C}$  ratios in foliar tissue. Foliar  $\delta^{13}\text{C}$  is a strong indicator of plant water stress and is very similar across these sites despite the variation in elevation between the Navajo and other sites (variation of  $<1\text{‰}$  across sites, data not shown).

### Soil Texture and Bulk Density

We measured soil texture as a volume percentage using a laser-light scattering method capable of measuring particles between 0.05 and 3,240  $\mu\text{m}$ . Organic matter was removed from sediment using a 30% solution of hydrogen peroxide prior to texture determination. Carbonate was removed using a 15% hydrochloric acid solution to eliminate any pedogenic carbonate in the soil. This treatment also removes any eolian carbonate and detrital calcite, which might be locally derived from carbonate bedrock. We measured bulk density using a Soil Moisture Equipment (Santa Barbara, CA, USA) model 0200 soil core sampler (Table 1).

### C and Nutrient Measurements

Soil and plant carbon and nitrogen content was measured with an EA 1110 CNS combustion analyzer (Thermo Electron Corporation, Waltham, MA, USA) at the Institute for Arctic and Alpine Research at the University of Colorado Boulder. Potassium, Mg, Ca, P, and Mn concentrations in rocks, soils, and plants were determined at the USGS in Denver. All samples were ground to pass through a 100-mesh sieve ( $< 150 \mu\text{m}$ ), and 0.2 g aliquots were dissolved using a four-acid ( $\text{HF}$ ,  $\text{HCl}$ ,  $\text{HNO}_3$ ,  $\text{HClO}_4$ ) total digestion procedure. Elemental concentrations were determined using Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES) and Inductively Coupled Plasma Mass Spectroscopy (ICP-MS) (Briggs 1996). Calcium

carbonate concentration was measured using a Chittick apparatus (Machette 1986) that uses acidification of a sample in 6 N  $\text{HCl}$  and subsequent measurement of the volume of liquid displaced by evolved gas.

### P Fractions and Exchangeable Cations

Both 0–5 cm and 5–10 cm samples were analyzed for soil P using a modified Hedley P fractionation method (Hedley and others 1982; Tiessen and Moir 1993), in which a sequential extraction of soil P is derived from one gram soil subsamples. The modified Hedley fractionation method begins with removal of phosphate ions from (1 g soil) solution with anion exchange resins (DynamBio, LLC, Madison, WI, USA) followed by extraction with 0.5 M sodium bicarbonate ( $\text{NaHCO}_3$ ) to remove the rest of the labile (plant available) forms of phosphorus. Subsequently 0.2 M sodium hydroxide ( $\text{NaOH}$ ) extracts moderately plant available inorganic P (Pi) and organic P (Po). The Pi and Po compounds of the  $\text{NaOH}$  fraction are held strongly by chemisorption to iron and aluminum components of soil surfaces or immobilized with microorganisms (Cross and Schlesinger 1995). Most mineral forms of phosphorus (apatite) are extracted by 1 M hydrochloric acid ( $\text{HCl}$ ). The stabilized forms of phosphorus are extracted via sonication using a small probe for 2 min at 75 W and re-extracting with 0.2 M  $\text{NaOH}$ . The Sonic Pi and Po are forms generally held inside Fe, Al, and Ca mineral surfaces. The most stable fraction (generally referred to as occluded or recalcitrant P) is extracted by  $\text{NaOH}$  fusion. This fraction is thought to be the least plant available, most stable Pi and Po. The extracts were diluted with DI water and neutralized. All P samples were analyzed by colorimetric techniques on a Lachat instrument with the Quickchem Method 10-115-01-1-A and 10-115-01-1-B (Lachat Instruments 2000) at the University of Denver. Three phosphorus pools were created by combining fractions (Cross and Schlesinger 1995) where the labile P pool consists of the resin plus bicarbonate-extracted organic and inorganic fractions. The biological P pool includes the bicarbonate organic,  $\text{NaOH}$  exchangeable, organic and sonicated organic P fractions, and the geochemical P pool includes all of the inorganic fractions.

Exchangeable cation concentrations (Mg, Mn, Ca, K) and total cation exchange capacity were determined by washing soil with a buffered solution of sodium acetate and then ammonium acetate as outlined by Hesse (1972). The sodium acetate solution was used to determine the exchangeability

of specific cations, and total cation exchange capacity was determined with the ammonium acetate solution. Concentrations from each washing were determined at the Laboratory for Environmental and Geological Studies, University of Colorado, with the use of ICP-AES.

## Statistical Design and Analysis

We examined bedrock geochemical differences using multi-way analysis of variance (MANOVA) with bedrock nutrients (Ca, Mg, K, and P) and metals (Fe and Al) as the dependent variables. Because sample size is heterogeneous across the four geologic settings, we do not present post hoc tests for bedrock chemistry.

Bulk element soil chemistry differences were evaluated using factorial MANOVA with Ca, Mg, K, Ca, Fe, and Al as dependent variables, and formation and soil depth as factors. Labile, biological, and total P were analyzed separately with a similar statistical design with formation and soil depth as the controlling factors.

We assessed plant stoichiometric variation along the bedrock gradient in two ways. First, we examined variation in stoichiometry across plant life forms using analysis of covariance (ANCOVA) to address foliar differences while accounting for variation in soil chemistry across the different geologic settings. Second, we examined a set of four species that co-occur across all four geologic settings to examine how particular species respond to underlying differences in bedrock settings.

For calculations of stoichiometric ratios, we reference each element to N. There are two reasons for picking N relative to C, P, or another element. First, N content in foliage does not vary significantly across the sites ( $P = 0.261$ ) thereby minimizing site-level bias into ratio calculations. Second, normalization against N rather than C is preferable because plant allocation to structural carbon can vary across plants species and life forms (for example, Knecht and Göransson 2004). We divided species into three vegetation life forms that included shrubs (*A. canescens* and *C. ramosissima*), forbs (*Salsola pestifer* and *G. sarothrae*), grasses (*S. comata*, *Hilaria jamesii* and *Sporobolus* sp.), and conifers (*Pinus edulis* and *Juniperus osteosperma*). We examined differences in stoichiometry across plant life forms with ANCOVA. Because not all species occurred across all settings, a factorial MANOVA design was not possible. Our general model structure used the E:N ratio (where E is P, Ca, Mg, or K) of plants as the dependent variable, plant life form as a categorical variable, and the corresponding

bulk soil element E concentration as a covariate. In each case we performed a two-step order of operation where we first tested for homogeneity of slopes (across plant functional types). If slopes were homogeneous, we then used ANCOVA as defined above to examine the role of life form and response to bulk and exchangeable soil elemental content. Where appropriate, we analyzed for differences between life forms by post hoc, unequal  $n$ , highly significant difference (HSD) tests, and regression analysis to examine the relations between foliar E:N ratios and soil-element content.

Four plant species grew in all four geologic settings examined in this study. The set of geologic settings and common species allows for a different analysis of stoichiometric responses than that afforded by the ANCOVAs above. Specifically, with this set of species we can ask whether the species-specific variation in foliar P, Ca, Mg, K, and N stoichiometry across all sites is similar. For this analysis we used MANOVA with bedrock type and plant species as the controlling factors. Dependent variables were P:N, Ca:N, Mg:N, and K:N. We carried out Tukey post hoc comparisons of differences across bedrock and species type where appropriate. For both ANCOVA and MANOVA statistical tests we examined variation across the four bedrock-derived nutrients (P, Ca, K, and Mg) to evaluate differences and similarities in species use of each element. Finally, to evaluate relative differences in plant chemistry and to compare normalized variation across elements (for example, Mg vs. Ca vs. P), we normalized differences between species in the following way. We calculated an average element:N ratio for each plant species (across all geologic settings) and then calculated each individual plant's deviation from that average calculated as  $(1 - \text{element:N}_{\text{plant}}) / \text{average element:N}_{\text{species}}$ . This calculation was carried out for P:N, Ca:N, Mg:N, and K:N ratios.

## RESULTS

### Bedrock Chemistry

Bedrock chemistry differed significantly across the four geologic formations (Wilks = 0.003,  $F = 7.514$ ,  $P < 0.001$ ). Concentrations of elements varied somewhat differently across the bedrock settings. For Fe and Al content, the Organ Rock and Moenkopi/Chinle sites were highest and Cedar Mesa and Navajo settings were lowest. Bedrock P paralleled Fe and Al across the four geologic types; it was highest in Moenkopi/Chinle, followed in order by the Organ Rock, Cedar Mesa, and Na-

**Table 2.** Bulk Element Content of Bedrock in Geologic Units

	Cedar Mesa ( <i>n</i> = 4)	Organ Rock ( <i>n</i> = 5)	Chinle/Moenkopi ( <i>n</i> = 3)	Navajo ( <i>n</i> = 2)
Al (%)	1.967 (0.260)	4.838 (0.637)	4.567 (0.731)	1.950 (0.250)
Fe (%)	0.460 (0.193)	1.945 (0.541)	1.867 (0.418)	0.285 (0.105)
Ca (%)	7.507 (3.496)	6.088 (1.651)	3.367 (0.788)	0.919 (0.882)
K (%)	1.300 (0.173)	2.538 (0.309)	2.433 (0.353)	2.000 (0.200)
Mg (%)	0.297 (0.068)	3.204 (1.100)	1.867 (0.318)	0.111 (0.029)
P (%)	0.017 (0.003)	0.038 (0.007)	0.054 (0.005)	0.010 (0.001)

Where possible, the samples are from outcrops near soils and vegetation sample sites (some sites did not have exposed bedrock outcrops). Values in parentheses are standard errors.

**Table 3.** Bulk Element Content of Surface Soils in Geologic Units

	Cedar Mesa	Organ Rock	Chinle/Moenkopi	Navajo
Al (%)	2.73 (0.56) A	4.30 (0.08) B	2.88 (0.32) A	2.75 (0.52) A
Fe (%)	0.92 (0.19) A	1.50 (0.14) B	1.14 (0.18) C	0.83 (0.21) A
Ca (%)	3.53 (0.89) A	3.26 (0.24) A	2.75 (0.50) A	0.66 (0.22) B
K (%)	1.65 (0.28) A	2.37 (0.14) B	1.81 (0.09) A	2.13 (0.30) B
Mg (%)	0.67 (0.15) A,B	1.60 (0.19) C	0.88 (0.17) B	0.35 (0.11) A
P (ppm)	390 (11) A	496 (8) B	410 (8) A	376 (11) A

Significant differences (Tukey post hoc test) in elemental content of soils at the  $P < 0.05$  level across bedrock formations are shown with contrasting letters within a row. Standard errors of site values ( $n = 3$ ) are indicated in parentheses.

**Table 4.** Exchangeable Cations in Surface Soils (0–5 cm) in Geologic Units

Cations	Cedar Mesa (0–5 cm)	Organ Rock (0–5 cm)	Chinle/Moenkopi (0–5 cm)	Navajo (0–5 cm)
Exchangeable Ca	1.06 (0.02) A, C	0.84 (0.18) A, B	1.33 (0.07) C	0.52 (0.08) B
Exchangeable K	0.17 (0.01) NS	0.16 (0.02) NS	0.21 (0.03) NS	0.16 (0.01) NS
Exchangeable Mg	0.07 (0.02) NS	0.07 (0.02) NS	0.12 (0.01) NS	0.07 (0.01) NS

All values are in units of mg exchangeable cation g soil<sup>-1</sup>. Significant differences determined through Tukey post hoc tests for each exchangeable element are shown by contrasting letters within a row. NS indicates non-significance. Standard errors of site values ( $n = 3$ ) are indicated in parentheses.

vajo sites. Calcium was variable across the bedrock types with very high concentrations (>6%) in the Cedar Mesa and Organ Rock settings, lower Ca in Moenkopi/Chinle (~3%), and very low concentrations in Navajo (0.3%). Potassium and Mg were highest in Organ Rock and Moenkopi/Chinle and lower to varying degrees in Cedar Mesa and Navajo (Table 2).

## Soil Chemistry

Soil element concentration varied with bedrock chemistry across the four sites (Wilks = 0.000,  $F = 31.2$ ,  $df = 18/31$ ,  $P < 0.001$ ) and concentrations generally increased with soil depth (Wilks = 0.012,  $F = 154.5$ ,  $df = 6/11$ ,  $P < 0.001$ ) although not equally across all the sites (site by soil depth interaction:

Wilks 0.011,  $F = 7$ ,  $df = 18/31$ ,  $P < 0.001$ ). Soil Fe and Al content were highest in the Organ Rock and Chinle/Moenkopi sites (Table 3). Calcium was four- to six fold lower in Navajo soils than any other sites, and Mg tended to be lowest on the Cedar Mesa and Navajo sites. Exchangeable cation concentrations generally paralleled bulk soil elemental content and were different across the four geologic substrates (Wilks = 0.054,  $F = 3.183$ ,  $df = 9/12$ ,  $P = 0.031$ ). Most of the differences in exchangeable cations were driven by very low concentrations of exchangeable Ca in the Navajo Sandstone site and high exchangeable Mg in the Chinle/Moenkopi site (Table 4).

For soil P, analyses of the labile, biological, and geochemical P pools showed only labile P was affected significantly by bedrock setting

**Table 5.** P Fractions for Surface Soils (0–5 cm) associated with the Listed Geologic Unit

	Fraction	Cedar Mesa	Organ Rock	Chinle/Moenkopi	Navajo
Resin	L, G	9.36 (1.04)	9.17 (2.28)	13.60 (1.12)	32.38 (1.92)
Bicarb Pi	L, G	8.14 (1.59)	20.66 (12.90)	13.32 (2.04)	5.31 (0.40)
Bicarb Po	L, B	18.11 (1.39)	13.97 (5.21)	13.75 (1.88)	21.36 (0.29)
NaOH Pi	G	3.07 (0.24)	3.07 (0.37)	3.76 (0.42)	3.58 (0.20)
NaOH Po	B	22.88 (0.21)	22.48 (0.94)	22.50 (0.55)	22.67 (0.47)
HCl Pi	G	109.16 (12.78)	147.75 (50.46)	139.85 (56.27)	43.01 (11.12)
Sonic Pi	G	2.29 (0.81)	1.91 (0.52)	3.22 (1.17)	2.91 (0.44)
Sonic Po	B	23.02 (0.84)	23.88 (0.66)	23.52 (0.94)	24.45 (0.71)
Residual P	G	383.95 (36.37)	425.55 (78.14)	417.19 (28.87)	415.17 (7.58)
<i>Labile P</i>	<i>L</i>	<i>35.62 (1.41) A</i>	<i>43.79 (9.58) A</i>	<i>40.67 (1.50) A</i>	<i>59.05 (2.19) B</i>
<i>Biological P</i>	<i>B</i>	<i>64.02 (2.42)*</i>	<i>60.33 (5.90)*</i>	<i>59.77 (2.95)*</i>	<i>68.48 (1.43)*</i>
<i>Geochemical P</i>	<i>G</i>	<i>516.00 (25.89)*</i>	<i>608.10 (91.79)*</i>	<i>590.94 (25.40)*</i>	<i>502.35 (15.70)*</i>
Total P		580.03 (24.13)	668.43 (96.69)	650.70 (28.33)	570.83 (14.62)

All values are in units of  $\mu\text{g P/g soil}$ . The rows with italicized entries at the bottom illustrate the labile pool (sum of resin, bicarbonate inorganic, and organic P fractions), biological pool (bicarbonate, NaOH, and sonicated Po fractions) and geochemical pool (Resin, Bicarbonate Pi, NaOH Pi, Sonic Pi, and residual fractions). The rows that contributed to the fractions are also designated with an L (labile), B (biological) or G (geochemical). Differences across sites were assessed for these three summed fractions using ANOVA and Tukey post hoc tests. In the case of significant site differences (labile fractions), site differences are illustrated by contrasting letters. An asterisk indicates that no site effect was found with ANOVA. Standard errors of site values ( $n = 3$ ) are indicated in parentheses.

(SS = 2,105,  $df = 3$ ,  $F = 12.25$ ,  $P < 0.001$ ; Table 5). The effect of bedrock on labile P was driven largely by 40–70% higher labile P in Navajo relative to the other settings. Neither biological P nor geochemical P changed with depth or across sites.

### Geochemical Controls on Soil P Content

Bedrock P was closely associated with Fe and Al content (Figure 2). A strong positive linear regression between P and Al was evident ( $P = 0.0012$ ,  $r^2 = 0.53$ ) and even stronger relations between P and Fe ( $P < 0.001$ ,  $r^2 = 0.80$ ). Labile P availability was inversely correlated to soil Ca ( $r^2 = 0.43$ ,  $P = 0.02$ ) at 5–10 cm depth in soils with a weaker relation in surface soils. Labile P was also weakly controlled by carbonate (Figure 2). There was no association between labile P and soil Fe or Al content at either 0–5 cm or 5–10 cm soil depths.

### Elemental Ratios Across Plant Functional Types

Foliar P:N ratios were strikingly different across the four plant life forms, but each life form responded similarly to underlying differences in soil labile P. Significant differences occur in P:N ratios across life forms (SS = 0.043,  $df = 3$ , MS = 0.014,  $F = 39.71$ ,  $P < 0.001$ ) and there is a significant positive relation between soil labile P and foliar P:N ratios (SS = 0.003,  $df = 1$ , MS = 0.003,  $F = 7.22$ ,  $P = 0.009$ ). The differences across life forms indicate that conifer P:N > forb P:N > shrub P:N > grass P:N (Table 6) (Appendix A see <http://www.springerlink.com>).

Plants on the Navajo Sandstone tended to have higher P:N ratios.

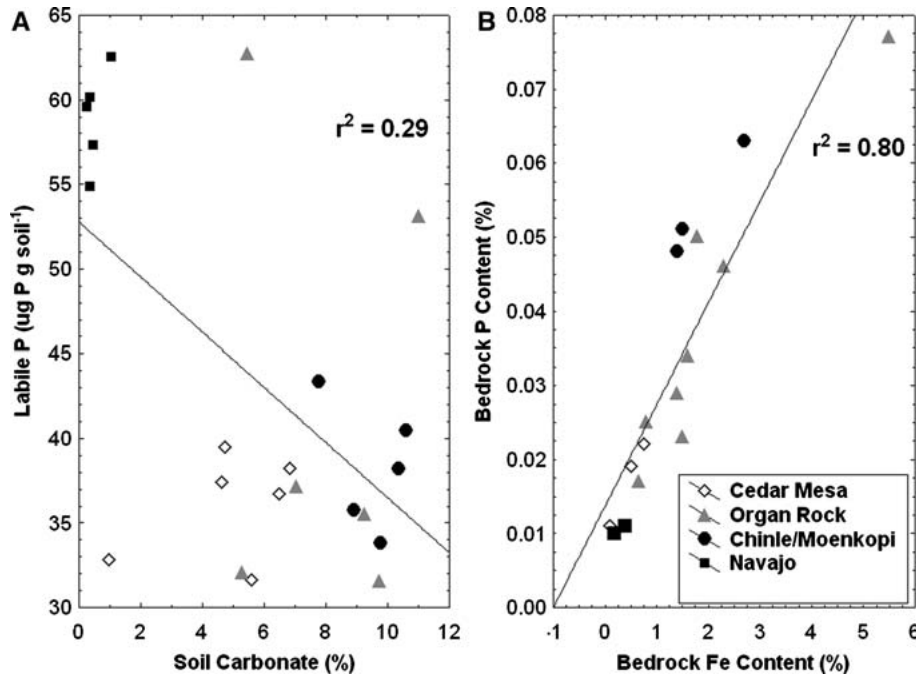
Calcium:N ratios were highly variable across life forms ranging from 1.41 for shrubs to 0.28 for grasses (SS = 15.76,  $df = 3$ ,  $F = 20.51$ ,  $P < 0.01$ ). However, foliar Ca:N did not vary with bulk or exchangeable soil Ca content. Conifers and forbs had intermediate values near 0.9 (Table 6). Plant K:N also varied by functional type with grasses and trees having the lowest K:N ratios (near 0.5) which is nearly three times higher than for forbs and shrubs (Table 6; SS = 11.12,  $df = 3$ ,  $F = 10.47$ ,  $P < 0.001$ ). Neither bulk nor exchangeable soil K was significant in the ANCOVA analysis. Finally, plant Mg:N ratios were highest in shrubs, lower in forbs and trees, and much lower in grasses (SS = 0.58,  $df = 3$ ,  $F = 20.25$ ,  $P < 0.001$ ), and they varied with bulk soil Mg (SS = 0.88,  $df = 1$ ,  $F = 9.32$ ,  $P < 0.003$ ) but not with soil exchangeable Mg.

Plant foliar N concentrations were used to normalize the foliar content of the other elements described above. For reference, foliar N values averaged 2.68 (SE = 0.13) % in shrubs, 2.08 (0.14) % in forbs, 2.69 (0.12) % in grass, and 1.12 (0.06) % in trees.

### Common Species Responses to Soil Biogeochemistry

For the four species occurring in all four geologic settings, both plant species and geologic setting controlled foliar nutrient ratios in our study area. Geologic setting strongly influenced plant elemen-





**Figure 2.** Relations among P, Fe, and carbonate. To illustrate how bedrock geochemistry may influence landscape variation in P, **A** shows the negative correlation between labile P in 5–10 cm depth soils and soil Ca content; this relation is probably due to in situ formation of secondary calcium phosphates in the Navajo Sandstone site (but note the lack of relationship in the other geologic settings). **B** shows the regression between bedrock Fe and bedrock P.

**Table 6.** Plant Stoichiometry across Three Life Forms

Plant Type	Foliar P:N	Foliar Ca:N	Foliar K:N	Foliar Mg:N
Forb ( <i>n</i> = 21)	0.089 (0.004) A	0.849 (0.092) A	1.216 (0.135) A	0.216 (0.032) A
Shrub ( <i>n</i> = 22)	0.079 (0.003) A,B	1.406 (0.154) B	1.359 (0.204) A	0.303 (0.024) B
Grass ( <i>n</i> = 27)	0.065 (0.002) B	0.282 (0.019) C	0.576 (0.024) B	0.094 (0.008) C
Conifer ( <i>n</i> = 13)	0.140 (0.010) C	0.941 (0.182) A,B	0.536 (0.025) B	0.199 (0.018) A

Values in parentheses are standard errors and the number of plants sampled is provided (*n*). Differences between plant life forms are determined from an Unequal N Highly Significant Differences (HSD) post hoc test following ANCOVA.

tal ratios (Wilks = 0.132,  $F = 6.36$ ,  $df = 12$ , error  $df = 66.44$ ,  $P < 0.001$ ). The species by geologic setting interaction was not significant, suggesting that the stoichiometry of the four common plant species responded similarly across the four distinct biogeochemical environments (Figure 3). We also did not find a species by geologic setting interaction when we carried out the same statistical tests using the element:C ratios (data not shown) indicating that both element:C and element:N ratios yield similar information about the role of geologic substrate in plant stoichiometry.

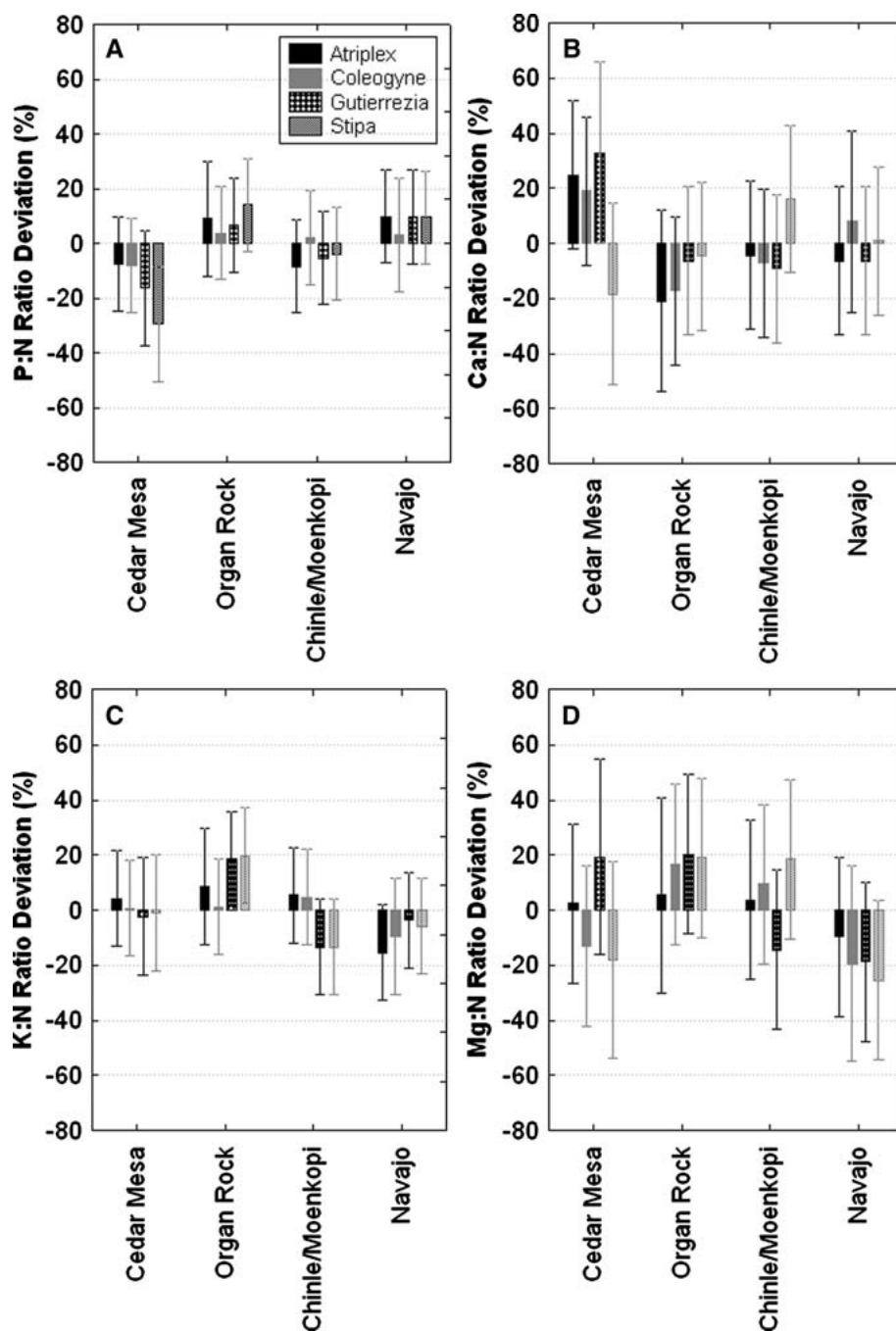
Tukey post hoc comparisons illustrate that many of the MANOVA differences are driven by foliar chemistry variation between the Cedar Mesa and Navajo settings. In general, Ca:N, Mg:N, and K:N ratios were lowest on the Navajo Sandstone sites, but the P:N ratios were highest. Plants at the Cedar Mesa sites had 30–100% higher Ca:N ratios compared to the other sites (Figure 4). Foliar chemistry differed across plant species (Wilks = 0.002,

$F = 57.52$  effect  $df = 12$ , error  $df = 66.44$ ,  $P < 0.001$ ) with patterns that reflected the ANCOVA analyses across functional types described above.

Although there are large differences in exchangeable nutrients across sites (up to 200%), normalized stoichiometry varied by only  $\pm 20\%$  across the landscape for any element:N ratio (Figure 3). Soil P availability, in particular, varied by almost two fold across sites, whereas the associated variation in foliar nutrient content across the sites was only 20%.

## DISCUSSION

The dryland ecosystems in and near Canyonlands National Park occur on substrates that vary substantially in P, K, Ca, and Mg. This variation is driven by differences in bedrock geochemistry associated with the different depositional conditions of these sedimentary rocks (for example, Dickinson and Gehrels 2003). The bedrock geo-



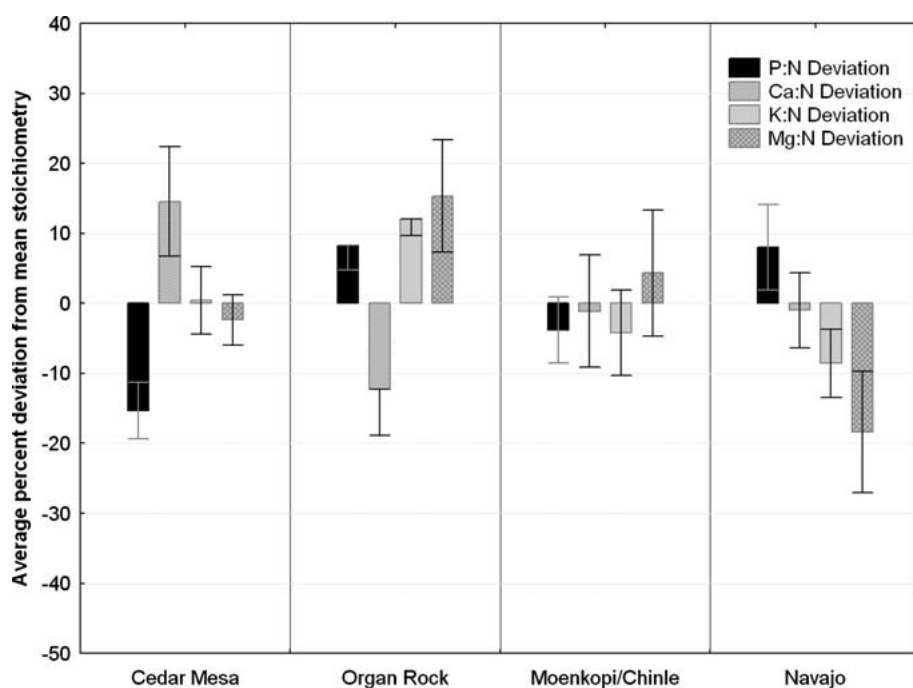
**Figure 3.** Average deviation in stoichiometry by common plant species across the four geologic/geochemical settings. The bars reflect the average deviation of plant stoichiometry from mean stoichiometry (all sites) in each study site. Positive values reflect higher element:N ratios and negative values indicate lower element:N ratios. Error bars represent standard errors.

chemical differences are reflected in bulk soil nutrients, and to a more varied degree, in soil nutrient availability and plant foliar nutrient concentrations. Whereas Mg, K, and Ca availabilities tend to parallel bulk soil (and bedrock) nutrient concentrations, P availability in soils appears to be largely controlled by Ca, and to a lesser degree, Fe and Al content. Plants that grow on these diverse bedrock environments respond similarly to underlying variation in soil nutrients despite broad variation in absolute foliar content and stoichiometry

across species and life forms. Plant foliar nutrient content varies with Ca and P availability but is not highly responsive to variation in exchangeable K or Mg. Foliar nutrient ratios were relatively similar ( $\pm 20\%$ ) for all elements considered even though there is large variation (up to 200%) in exchangeable Ca and P across sites.

### Bedrock and Soil Element Content

Previous work in desert ecosystems has illustrated the importance of Ca–P relations in plant nutrient



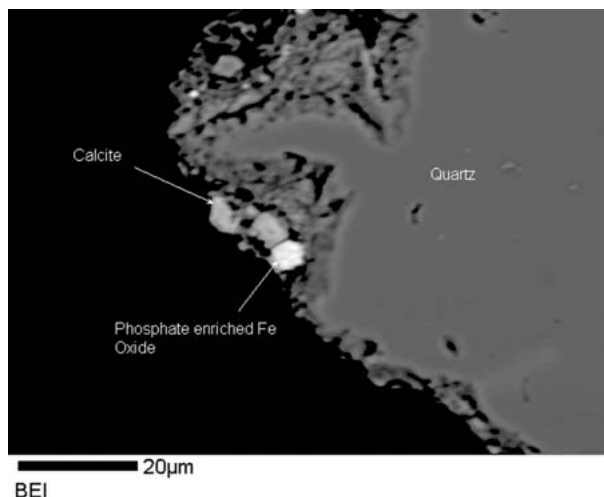
**Figure 4.** Average deviation in stoichiometry across the four geologic/geochemical settings. The bars reflect the average deviation of plant stoichiometry from mean stoichiometry (all sites) in each study site. Positive values reflect higher element:N ratios and negative values indicate lower element:N ratios. Values do not sum to zero across sites because each individual plant is normalized to the average foliar nutrient ratio of the same species in all sites. Those values are then averaged for a site. Error bars represent standard errors.

uptake (Lajtha and Schlesinger 1988a, and b). In desert soils, the geochemical sequestration of P into secondary calcium phosphates should dominate the cycling of available P because of the low solubility of secondary calcium phosphate in alkaline soils (Frossard and others 1995; Carreira and Lajtha 1997). This pattern of strong Ca control over P availability is borne out in the Navajo and Cedar Mesa sites, which are both eolian-formed sandstone settings. The most P-poor setting in this study is the Cedar Mesa site; an environment that has high  $\text{CaCO}_3$  and low bedrock P. In contrast, the Navajo Sandstone setting has very low  $\text{CaCO}_3$  and the highest available P of all the sites despite very low bedrock P values. Concentrations of the HCl Pi fractions in the modified Hedley extractions on these two eolian sandstones confirm the importance of secondary calcium phosphate formation in controlling P availability. However, the relation between labile P and soil Ca or carbonate is non-existent if the Navajo sites are excluded from the regression (despite relatively high carbonate content in the Organ Rock and Moenkopi/Chinle settings). These relatively complex controls over P availability probably come about because bedrock P, Fe and Al content also influence P content and availability in some geologic settings near Canyonlands National Park particularly in the Chinle/Moenkopi and Organ Rock sites. The bedrock P content in these sites is substantially higher than in the eolian sandstones and it appears the P is associated with Fe oxide minerals. These same Fe oxide

minerals may also play a critical role in the control of P availability in soils where they continue to have very high sorption affinity for  $\text{PO}_4^{3-}$  (Ryan and others 1985; Carreira and others 1997; Samadi and Gilkes 1998).

Although  $\text{CaCO}_3$  clearly plays a role in control of P availability in some of the soils near CNP, the actual geochemical mechanisms of P stabilization may be more complex than what is implied by the modified Hedley fractionations. For example calcite coatings on soil surfaces may bind P-bearing minerals, particularly Fe and Al phosphates. This stabilization is shown for the Cedar Mesa site in an electron microprobe image (Figure 5). Some iron phosphate minerals may be soluble at low pH once released from  $\text{CaCO}_3$  coatings suggesting that the actual geochemical mechanisms of P stabilization and release are not entirely clear (Frossard and others 1995). In addition, the size and reactivity of carbonate particles can be important for P cycling in calcareous soils (Holford and Mattingly 1975; Lajtha and Bloomer 1988).

The patterns of P availability and potential mechanisms of release and stabilization differ from the common articulated model for P weathering in soils. In ecosystems that develop from igneous rocks, P weathers from primary forms (such as apatite) into secondary mineral phases and then is finally stabilized into occluded forms on the surfaces of Fe and Al oxides (Walker and Syers 1976; Crews and others 1995). However, in sedimentary (and perhaps in metamorphic settings), the most



**Figure 5.** Electron microprobe image of a particle from surface (0–5 cm) soil derived from the Cedar Mesa Sandstone. The image shows a P-rich Fe oxide mineral embedded in calcite cement at the margin of a detrital quartz grain.

unavailable forms of P may be found in secondary apatite minerals (for example, Frossard and others 1995) and the major sources of P for weathering may be found in Fe and Al oxide forms of P. In the area near CNP, the strong association between bedrock Fe, Al, and P content suggests that bedrock P is dominantly associated with Fe and Al. As these materials weather, the release of Ca into soils then controls P availability to plants if soil Fe and Al content is low. If the Fe and Al content of soils is also high, as in the Moenkopi/Chinle and Organ Rock settings, then the actual geochemical controls on P availability remain complex and somewhat uncertain (though they likely involve a combination of Fe, Al, Ca, and P associations). Atmospheric dust inputs add an additional source of variation through significant concentrations of P that can be deposited to desert soils surfaces, although the mineral form of these P inputs remains unknown (Reynolds and others 2006).

Soil variation in Ca, K, and Mg across the study sites is also substantial. As mentioned above, there are broad gradients in bulk and exchangeable Ca content and significant variation in bulk-soil Mg content. In contrast, K content of soils is less variable. As with P, the variation in bedrock and soil concentrations of these rock-derived nutrients is related closely to the depositional environments of the different bedrock units in the region. Even within eolian sandstones, the Ca and Mg content of bedrock can vary with the composition, leaching and biological history (presence of organisms) of

the sediments it formed from (McBride and Parea 2001). Within soils, the availability of base cations is somewhat disconnected from bedrock concentrations and appears to parallel site variation in CEC and soil texture. This work suggests that there may be significant site level variation in the availability of base cations associated with the strong geomorphic (and land use driven) gradients in soil texture found in this region (Neff and others 2005; Reynolds and others 2006).

## Plant Foliar Chemistry

The Colorado Plateau region has a wide range of endemic, rare plants and this phenomenon is often attributed to the geology of the region (Welsh 1978; Kruckeberg 1986; Nelson and Harper 1991; Kelso and others 2003; Van Buren and Harper 2003). However, there is still little information about the chemical characteristics/demands of particular plant species that predispose them to particular geologic substrates. For all the elements considered here, including P, Ca, K, and Mg, there was a similar limited response of foliar nutrient ratios to underlying differences in nutrient availability across substrates for the four plant life forms, as well as for individual species. The similar response to different bedrock chemistry differences occurs despite very large differences in absolute stoichiometric ratios across the life forms and individual species. In other words, the absolute foliar content of the growth forms studied here appears to have little impact on the response of the growth forms to variation in soil nutrient availability across sites. Among growth forms, one strong trend was that grasses tended to have lower element:N ratios than the other life forms driven largely by higher concentrations of foliar N.

The Navajo and Organ Rock settings had the highest average P availability and this was reflected in P:N ratios that were about 8% higher than the average across all sites. The other two settings had 4–15% lower P:N ratios than the average, placing the overall variation in P:N ratios in response to soil nutrient differences at about 20%. By way of comparison, there is a 200–300% variation in P:N stoichiometry observed across broad latitudinal gradients even in similar plant functional types (McGroddy and others 2004; Reich and Oleksyn 2004). Ratios of Ca:N, K:N, and Mg:N ratios were generally similar to, or slightly higher than, means of these ratios in litter worldwide (Knecht and Göransson 2004) suggesting that these cations are present in relatively high abundance in these dry-land sites. Despite this relative abundance, base

cation:N ratios did show 20–25% variation across study sites with approximately 30% variation in Mg:N ratios. As with P:N ratio variation, 25–30% variation across sites is relatively small when compared to variation in other studies. For example, in a literature review of Ca:N, K:N, and Mg:N ratios for coniferous, deciduous and herbaceous groups, Knecht and Göransson (2004) found broad variation (up to two times) in Ca:N and K:N ratios and greater than 50% variation in Mg:N ratios (exclusive of outlier values). Compared to these values, the variation across sites in this study is relatively small. Finally, in this study absolute element:N ratios were not good predictors of how plants respond to variation in soil nutrient content and as with P:N ratios, the variation of individual species and/or life forms in response to soil nutrient content tended to be similar. Across the sites studied here, neither Ca:N nor K:N ratios followed exchangeable Ca or K values but Mg:N appeared more closely related to exchangeable Mg. The potential importance of Mg to desert plant productivity has also been observed in the Mojave Desert where Mg, N, and P added together, significantly increase primary productivity of *Atriplex* (James and others 2005).

There is evidence that foliar stoichiometry may provide an indication of the element that limits productivity. A study of European wetland plant species suggests that foliar N:P ratios below 14 indicate N limitation whereas those above 16 indicate P limitation (Koerselman and Meuleman 1996). The existence of a single critical ratio above or below which nutrient limitation occurs requires a relatively high degree of biochemical consistency across a range of species and environments. Work in desert environments suggests that, even within a particular growth form (shrubs), there is not a consistent foliar N:P ratio that indicates N versus P limitation (Drenovsky and Richards 2004). In this study, the N:P ratios of plants ranged from 7 to 15 across growth forms present in the same biogeochemical settings. In most cases, these ratios would be interpreted as representing N limitation to productivity. We suggest that simple ratio-based assessment of nutrient limitation be applied in deserts with caution for two reasons. First the substantial variation in N:P ratios across growth forms present in the same soil nutrient environment in this study raises questions about the applicability of a single ratio to species that may have very different baseline requirements for essential nutrients. Second, in their study of desert shrubs, Drenovsky and Richards (2004) suggest three potential mechanisms why a single N:P indicator of limitation may not occur in desert environments.

These mechanisms include water and nutrient co-limitation, lack of stoichiometric plasticity or lower overall tissue nutrient requirements. This study suggests that plants along this local fertility gradient on the Colorado Plateau may simply have limited phenotypic capacity to respond to variation in soil-nutrient content, consistent with adaptations to nutrient-poor environments (Chapin 1980; Bloom and others 1985). Alternatively, these plants may be well adapted to the local conditions of the Colorado Plateau and therefore able to maintain consistent foliar nutrient concentrations, despite relatively low soil nutrient availability in some of the bedrock, settings.

There are a number of ways to assess how plants use nutrients including fertilizer studies, meta-analysis of data that span broad geographic areas and the approach used here; comparison of nutrient use across natural gradients in soil nutrient availability. A comparison of these approaches suggests that in many cases, plants exhibit larger variation in foliar chemistry in response to fertilization studies or during comparison of species or functional group chemistry across broad geographic gradients (for example, McGroddy and others 2004), than are observed along local gradients in soil fertility. Other studies of plant foliar responses to local fertility gradients show relatively similar foliar nutrients despite differences in soil nutrient availability (for example, Bowman and others 2003) and there is evidence that species-specific nutrient use traits (rather than flexible nutrient use) dominate how plants respond to edaphic gradients (for example, Knops and Koenig 1997). If plant nutrient use, even within similar species or growth forms, depends on adaptations to local biogeochemical conditions that may limit plasticity in foliar nutrient content, then foliar nutrient content or ratios will not be consistent or reliable predictors of plant/soil nutrient relations. Similarly differences in foliar chemistry across broad latitudinal gradients may represent differences in plant adaptation to particular environments rather than an indication of contemporary underlying nutrient content.

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